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WHY ROOST AT THE SAME PLACE? EXPLORING SHORT-TERM FIDELITY IN STAGING SNOW GEESE

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Abstract. When a communal roost is large relative to foraging distances, variance in foraging success may affect the positioning of the birds within the roost and we should expect fidelity to positions that improve foraging success. We explored fidelity of Snow Geese (*Chen caerulescens*) to three sections of a 5-km^2 roost in flooded lowlands during their spring stopover in Quebec. From 1998 to 2000, we located 166 radio-tagged geese on 1077 occasions. Fidelity rates were higher than expected by chance in all sections in 1998, in two in 2000, but in none in 1999. Fidelity increased with the number of birds using a section, suggesting a positive effect of conspecific attraction. We tracked 292 foraging trips of 108 radio-tagged geese; birds from different sections tended to forage in specific directions. Average distance to foraging sites saved by appropriate choice of a section varied between 7 and 17%, depending on the section. However, distance traveled over 2 successive days did not decrease when geese switched from roosting in one section to another, suggesting that minimization of foraging-trip distance may stem simply from the spatial organization of foraging trips in order to reduce travel distance to food patches. Higher fidelity rates were associated with shorter travel distance in only one section of the roost, and dominant birds arriving early in the season tended to be more faithful to this section. We conclude that conspecific attraction, reduction in travel costs to foraging sites, and individual variation in dominance determine roost positioning and fidelity concurrently.

Key words: Chen caerulescens, *farmlands*, *foraging*, *migration*, *roost*, *Snow Goose*, *spring staging.*

¿Por Qué Usar los Mismos Dormideros? Explorando la Fidelidad de Corto Plazo en *Chen caerulescens*

Resumen. Cuando un dormidero es grande con relación a las distancias de forrajeo, la varianza en el éxito de forrajeo puede afectar la posición de las aves dentro del dormidero y deberíamos esperar fidelidad a las posiciones que mejoran el éxito de forrajeo. Exploramos la fidelidad de *Chen caerulescens* para con tres secciones de un dormidero de 5 km^2 en tierras bajas inundables durante la parada primaveral en Quebec. Desde 1998 a 2000, localizamos 166 gansos marcados con radio transmisores en 1077 ocasiones. Las tasas de fidelidad fueron más altas que lo esperado por azar en todas las secciones en 1998, en dos en 2000, pero en ninguna en 1999. La fidelidad aumentó con el número de aves que usaron una sección, sugiriendo un efecto positivo de atracción coespecífica. Seguimos 292 viajes de forrajeo de 108 gansos marcados con radio collares, y observamos que las aves de diferentes secciones del dormidero tendieron a forrajear en direcciones específicas. La distancia promedio del viaje de forrajeo resguardada por la elección apropiada de una sección del dormidero varió entre 7 y 17%, dependiendo de la sección. Sin embargo, la distancia viajada durante dos días sucesivos no disminuyó cuando los gansos cambiaron de una sección a otra del dormidero, sugiriendo que la minimización de la distancia del viaje de forrajeo puede simplemente derivarse de la organización espacial de los viajes de forrajeo para reducir la distancia de viaje a los parches de alimento. Las mayores tasas de fidelidad estuvieron asociadas con una distancia de viaje menor en sólo una sección del dormidero y las aves dominantes que llegaron más temprano en la estación tendieron a ser más fieles a esta sección. Concluimos que la atracción coespecífica, la reducción en los costos del viaje a los sitios de forrajeo y la variación individual en la dominancia determinan conjuntamente la posición y la fidelidad a la posición en el dormidero.

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INTRODUCTION

The sustained use of the same location by a given individual, referred to as site fidelity, depends on the availability and quality of the site and its function (e.g. breeding, foraging, or roosting). Fidelity rate may vary strongly by spatiotemporal scale. For instance, a colonial bird may be faithful year after year to a colony but not to a nest site (Lecomte et al. 2008). While a few studies have dealt with roost fidelity in the context of multi-roost systems (Morrison and Caccamise 1985, Giroux 1991), fidelity to positions within a roost has, however, received much less attention. Both phenomena have important implications for the spatiotemporal dynamics of roosts, but their determinants are poorly known. So far, emphasis has been put on the evolutionary origin of communal roosting based on the potential advantages for food finding (Barta and Giraldeau 2001) and the anti-predator processes associated with large flocks (Hamilton 1971).

We investigated the day-to-day fidelity of Greater Snow Geese (*Chen caerulescens atlantica*) to different sections of a roost used during spring migration at a major staging area in southern Quebec. The geese roost in contiguous flooded fields that cover 2–5 km^2 and fly to feeding sites located throughout 2500-km^2 landscape dominated by agricultural lands. They spend more time feeding in plowed cornfields, which are the most abundant foraging habitat (Béchet et al. 2004). However, they prefer to feed in unplowed cornfields left in stubble, which are much less available because most fields are plowed in fall. Waste corn is more abundant in stubble, but its availability in both types of field is highly variable (Giroux and Bergeron 1996). Hence, searching for a rich patch of food may be costly, but the expected returns are high because corn grains have a high energy value (Frederick et al. 1987). Because the geese deplete the corn rapidly, they rarely use the same fields over more than 2 or 3 successive days. When leaving the roost to forage, the birds therefore often have to look for a new field. While in flight, geese may obtain information from their congeners on the availability of cornfields for future foraging.

All other things being equal, birds should prefer locations within a roost that reduce travel distances to food patches. This hypothesis stems from the same geometrical reasoning on which Horn (1968) based his central-place foraging hypothesis, except that it is the position within the roost rather than the nest site that becomes the individual's fixed base of operation. Hence, fidelity to some sections of a roost may arise because birds explore the same foraging area repeatedly and thus occupy the section of the roost closest to that area. Yet, if searching leads a bird to food patches that are closer to another part of the roost, it may switch position within the roost to minimize travel distance to this new foraging area. Switching may also be a decision to explore new foraging areas if an individual's intake rate reaches a level lower than expected from previous experience (Charnov 1976).

We first explored how plowed and stubble cornfields, the two main foraging habitats geese use in this area, were spatially distributed within the landscape. Second, we established whether fidelity rates of geese to different sections of the roost were higher than expected by chance. We then tested the predictions that travel distances and directions of geese using different sections of the roost should differ. In a third step, we examined the hypothesis that fidelity rates are related to variations in searching efficiency from different sections of the roost. We expected high fidelity rates to roost sections that minimized travel distance to food patches. We also predicted that distances traveled in 2 successive days should decrease if geese had switched from one section of the roost to another. Individual differences, such as a bird's level dominance and whether it is paired, may influence competitive ability (Gregoire and Ankney 1990, Stahl et al. 2001) and thus selection of positions within the roost. We predicted that paired and dominant geese should show higher fidelity rates to roost sections that minimize travel cost than should unpaired or subordinate individuals.

METHODS

STUDY AREA

In spring, Greater Snow Geese that winter in the United States stop in southern Quebec, where they fatten up before undertaking their final migration to their arctic breeding grounds (Gauthier et al. 1992). The main staging area is located near Baie-du-Febvre, where up to 500 000 geese can roost in temporarily flooded lowlands along the shore of Lake St. Pierre (Fig. 1). This lake is an enlargement of the St. Lawrence River, and rising water levels associated with spring run-off flood the adjacent lowlands. Some sections are managed to retain water for staging waterfowl. In years of high water levels, unmanaged contiguous fields are also flooded, thereby increasing the extent of the roost, especially toward the west.

We divided the roost into three sections delimited by gravel roads, dikes, or other landscape features (Fig. 1). The western, central, and eastern sections covered 2.8, 0.9, and 0.9 km^2, respectively. Water levels were lower in 2000, reducing the area of flooded lowlands. We therefore shifted the three sections eastward, reducing the western, central, and eastern sections to 0.9, 0.5, and 0.4 km^2, respectively. This change should not affect our results because it is the relative position and characteristics of each section within the roost that are important, and these remained unchanged. Moreover, the relative position of the three sections in relation to the feeding sites also remained the same throughout the study.

Geese leave the roost en masse at dawn in search of food patches scattered in an area of approximately 40 × 63 km southeast of Baie-du-Febvre (Fig. 1). Departures are synchronized, and most geese have left within 30 min after sunrise. During the study, geese spent 28 and 39% of their feeding time in stubble and plowed cornfields, respectively, 20% in hayfields, and 13% in other crops (Béchet et al. 2004).

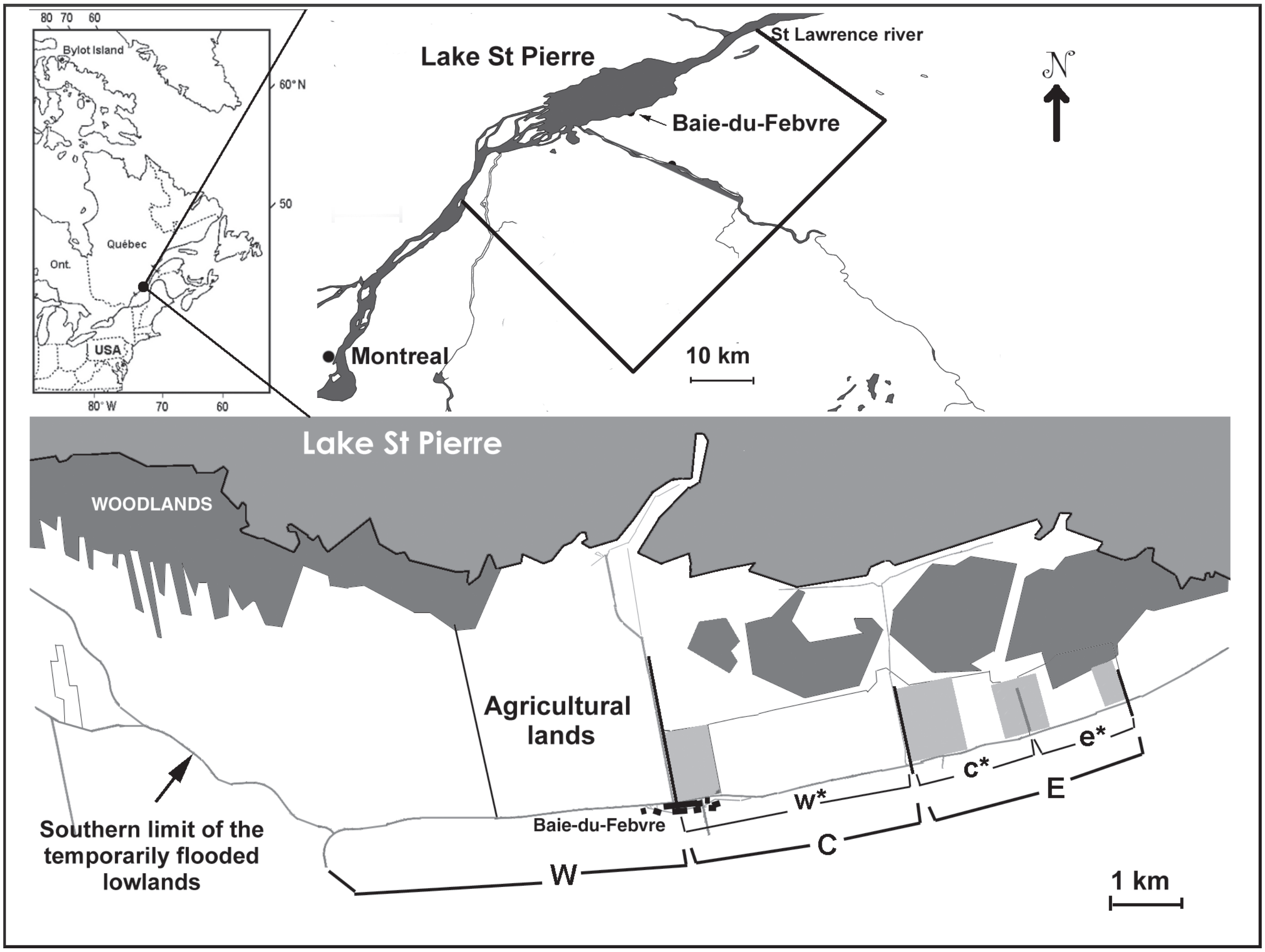

FIGURE 1. Map of the Lake St. Pierre region (Quebec, Canada) with the Baie-du-Febvre roost. The thick line in the upper right panel represents the approximate limits of the foraging area the geese used 1997–1999. Enlarged are the flooded lowlands with the western (W), central (C), and eastern (E) sections of the roost defined. In 2000, the three sections (denoted by *) were shifted eastward because of limited flooding. The light gray portions of the flooded lowlands are managed to retain water for staging waterfowl.

SAMPLING OF AGRICULTURAL HABITATS

In spring 1999 and 2000, we sampled 104 randomly located 1-km^2 plots to characterize the habitat available for feeding geese. Crop types (prevailing in the previous year) and their condition were mapped on 1:15 000 black-and-white aerial photos by inspection of each field from the ground after snow melt and prior to cultivation. The georeferenced maps were then digitized, and the area covered by each crop was computed. We considered only the habitats known to be used by geese in determining their relative abundance.

MARKING AND TRACKING OF GEESE

Between 1996 and 1999, a total of 310 adult female Greater Snow Geese were fitted with a VHF radio-collar on their breeding grounds at Bylot Island, Nunavut (73° 00′ N, 80° 00′ W). Using corral traps (Demers et al. 2003), we captured small family groups (<30 geese) consisting of molting adults with their 25- to 35-day old young. Radios weighed 59.3 ± 0.5 g (i.e., 2.5 ± 0.1% of the female's body mass), had a 1-year life expectancy, and a signal detectable from 1 to 2 km on the ground. Females radio-marked within the same group did not migrate at the same time nor use the same staging sites (Giroux, unpubl. data).

We tracked radio-tagged geese for four years (1997–2000) during their spring staging around Lake St. Pierre. The first geese arrived at the onset of snowmelt (15 March–1 April). In 1997, we did not systematically record the location where each goose roosted but obtained locations of departure for a sample of foraging trips. From 1998 to 2000, we recorded the section of the roost used by the tagged geese every morning before dawn and every second evening after dusk. Randomly chosen radio-tagged geese were tracked every morning by car from roost to food patches. The locations of the geese in the fields were recorded on 1:50 000 maps to the nearest 100 m. Finally, in 1999 and 2000, we counted from the ground the total number of geese present in each section daily, before their morning departure.

Whether radio-tagged females were paired or single was determined through visual observations (Bêty et al. 2004). Displacements by conspecifics and kleptoparasitism observed on food patches were used to establish dominance ranks. Aggressive encounters involving radio-tagged females or their mates with other foraging geese were classified as won, lost, or tied according to whether the male or the female displaced a goose, was displaced by another goose, or none of the geese finally moved from their initial position (Stahl et al. 2001). As the proportion of interactions won reaches an asymptote around 10 encounters (Bêty et al. 2004), we required a minimum of 10 observations involving a given individual (either male or female) to determine its rank. For paired females, we used the higher of the two dominance ranks of the members of the pair. Finally, we controlled for arrival date and length of stay of the birds in the Lake St. Pierre region, as these variables might influence the settlement of geese within an already established roost. Relative arrival date was calculated as the difference between an individual's arrival date and the median arrival date of all marked geese each year.

STATISTICAL ANALYSES

We first assessed whether the similarity of the 1-km^2 plots, in terms of area of stubble or plowed cornfield, varied linearly (Pearson correlation) or nonlinearly (Spearman correlation) with distance at different spatial scales by using a Mantel correlogram based on Euclidean dissimilarity matrices. Inferential tests on Mantel statistics were two-sided and based on 10 000 permutations of the rows and columns of the standardized dissimilarity matrix (Goslee and Urban 2007). Using both omnidirectional and directional variograms, we further characterized the spatial structure underlying the distribution of stubble and plowed cornfields measured in 1-km^2 plots separately. An omnidirectional variogram quantifies how the variance of the area covered by a habitat type taken within pairs of points separated by a given distance varies as a function of distance. It assumes isotropy, that is, locations are independent of direction. On the other hand, a directional variogram considers pairs of points along specific directions (0°, 45°, 90°, and 135° in our case). The assumption of quasi-stationarity was verified and controlled for by means of trend-surface analysis based on polynomial regressions (Legendre and Legendre 1998). We computed Mantel correlograms and variograms with R 2.8.1 (R Development Core Team 2008) and the add-on libraries ecodist 1.2.2 (Goslee and Urban 2007) and geoR 1.6.23 (Ribeiro and Diggle 2001), respectively.

We defined the daily fidelity rate (F_i) of an individual to a given roost section i as the number of consecutive locations n_i in section i divided by its total number of locations N_i in that section: $F_i = n_i / N_i$, where $N_i \geq 1$. Hence, the fidelity rate tends asymptotically to 1 as the length of stay of a bird in the same section increases. To determine whether this fidelity was genuine or resulted simply by chance, we first generated 1000 random sequences of night locations for each season by resampling the observed sequence of night locations for the length of the season. Every night, each radio-tagged bird was randomly assigned to one of the available sections of the roost. To avoid overuse of some sections relative to the overall number of geese they could support, we defined a section as unavailable when it was used the number of times equal to the observed number When geese stopped using a section before the end of the season, this section was also removed. For each random sequence, we calculated section-specific fidelity rates. We compared the observed values to the random distributions generated by resampling (Manly 1991). P-values were based on one-tailed tests relative to the alternative hypothesis that observed fidelity rates were higher than expected by chance.

For each foraging trip of a radio-tagged bird, we calculated the distance traveled by assuming that the bird left from the center of the section where it was located in the morning. We also calculated the azimuth of the food patch relative to the center of the roost. We used generalized linear models with a normal error distribution and identity-link function to test the effects of year and roost section on distances and directions of foraging locations.

Next, we estimated the probability that a bird had chosen a section of the roost that minimized foraging trip distance by first calculating all potential distances of foraging trips on the basis of the different roost sections and each observed foraging location. The actual distances traveled by the bird were then compared to the potential distances and scored 1 if they were shorter, 0 otherwise. We used logistic-regression models to test whether the probability of an appropriate choice differed by roost section for each year of the study. When the roost section chosen by the geese was appropriate, we estimated the distance saved relative to the farthest roost section available. Finally, we calculated the difference between distances traveled by geese tracked for 2 successive days to test the prediction that roost-section changes should reduce the distance traveled. We used generalized linear models with a normal error distribution and identity-link function to test the effect of switching or staying on the distance difference.

We computed section-specific fidelity rates for individuals of known pair status and dominance level. We analyzed each section separately because fidelity rates to each section were independent ($r_s = -0.26$ to 0.20, $n = 37$, $P > 0.10$). Because these rates had a clear bimodal distribution, a goose was classified as faithful if its fidelity rate was above the median and as a switcher if its rate was below. For each roost section, we fitted several logistic-regression models including the effects of year (YEAR), pair status (PAIR), dominance (DOM), relative arrival date (RELA), length of stay in the staging area (LENGTH), and two interactions (DOM × PAIR, DOM × RELA) to explain an individual's fidelity rate. Finally, too few radio-tagged geese were still with their young in the spring for the number of young to be included as an explanatory variable.

We checked all continuous response variables for normality of residuals and homoscedasticity. When these assumptions were not met, we tested the significance of the interaction term with the aligned-rank test (ART, Salter and Fawcett 1993) and the significance of main effects with rank-transformed raw data (Potvin and Roff 1993). All models were fitted with PROC GENMOD (SAS Institute 1999). Some individuals were tracked during several foraging trips, leading to pseudoreplication (Aebischer et al. 1993). We therefore attributed a weight inversely proportional to the number of times an individual was tracked so that the sum of the weights equaled 1; each individual thus contributed to only one degree of freedom.

Model selection was based on Akaike's information criterion with the bias adjustment for small samples, AIC_c (Burnham and Anderson 1998). We present the AIC_c differences, ΔAIC_c, for the model with the lowest value and the AIC_c weights, w_i, as an index of relative plausibility for comparison of models. To assess the effect of roost section on different response variables, we compared models including two roost sections with models in which a combination of two roost sections (western-central, western-eastern, and central-eastern) was pooled into one that transposes the issue of multiple comparisons into an a priori model selection. For logistic models, the reliability of the general model was measured by a goodness-of-fit test based on Pearson χ^2 (McCullagh and Nelder 1983). We present means ± 1 SE unless stated otherwise.

RESULTS

FIDELITY TO ROOST SECTIONS

From 1998 to 2000, we located respectively 59, 56, and 59 radio-tagged geese at least once in the roost of Baie-du-Febvre, for a total of 1077 locations. The distribution of marked geese reflected the distribution of the whole flock among the three sections, as shown by the total number of geese counted daily in 1999 and 2000 (Fig. 2). The length of stay of individual geese in the area was highly variable (range 2–32 days), and the total length of stay by all radio-tagged geese lasted 42 days in 1997, 36 days in 1998, 17 days in 1999, and 23 days in 2000. Therefore we generated the yearly random sequences of night locations for these corresponding numbers of days.

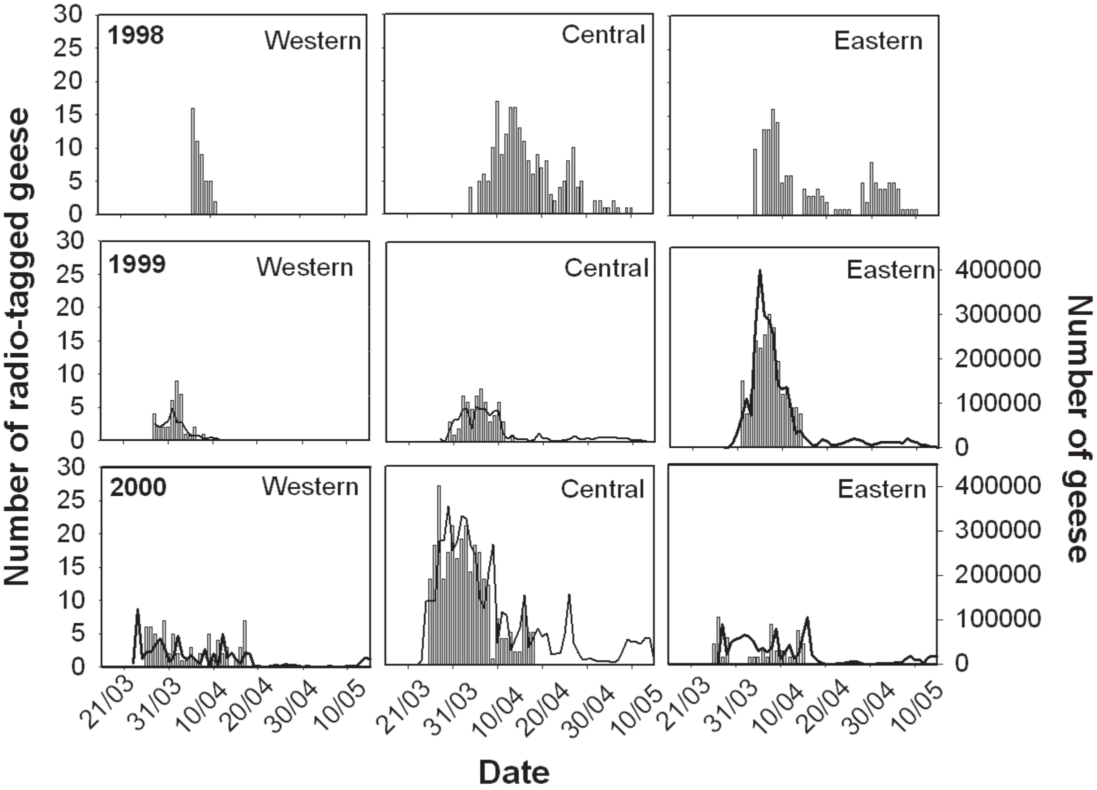

FIGURE 2. Daily counts of spring staging Greater Snow Geese in 1999 and 2000 (solid line) and number of radio-tagged geese from 1998 to 2000 (vertical bars) in three sections of the Baie-du-Febvre roost.

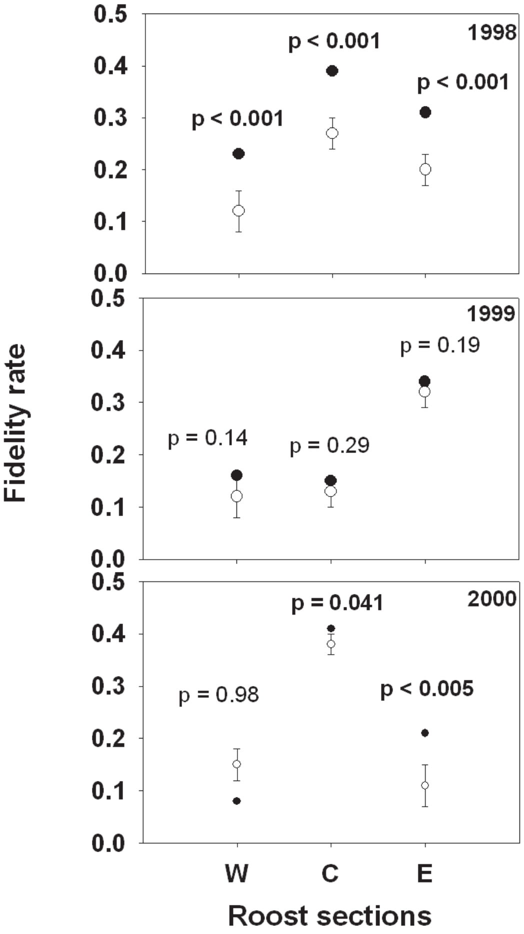

FIGURE 3. Daily fidelity rates of staging radio-tagged Greater Snow Geese to three roost sections at Baie-du-Febvre, 1998–2000. Mean (± SD) of 1000 randomly generated fidelity rates (empty circles) and mean observed fidelity rate (black circles). *P*-values are based on one-tailed tests relative to the alternative hypothesis that observed fidelity rates were higher than expected by chance.

Geese moved between roost sections during the night in 6% (annual range 4–10%) of the paired evening/morning observations ($n = 380$). For nights with an evening location only (<21% of the cases between 1998 and 2000), we used this location to evaluate roost-section use but discarded these observations when analyzing foraging trips. Fidelity rates were higher than expected by the random-distribution model for all sections in 1998 but for none in 1999 (Fig. 3). In 2000, fidelity rates were higher than expected for the central and eastern sections. Each year, the radio-marked geese were more faithful to sections that supported the greatest number of roosting birds (1998: central, 1999: eastern, 2000: central; Fig. 2). As a whole, fidelity rates were positively related to the total number of radio locations obtained each year in each section, which is an index of bird use ($r_s = 0.73$, $n = 9$, $P = 0.02$).

SPATIAL ORGANIZATION OF FORAGING TRIPS

The crop grown in a given field may vary annually according to usual farming practices, but the crops' relative abundance over the whole landscape varied little between 1999 and 2000. As a whole, 65% of the area was covered by agricultural lands that included plowed cornfields (37%), hayfields (28%), plowed hayfields (21%), plowed fields of small cereals (8%), and stubble cornfields (6%). Mantel correlograms indicated that composition of foraging habitat within 1-km^2 plots was weakly but significantly ($P < 0.05$) positively autocorrelated up to a scale of approximately 15 km in both years. There was, however, no sign of negative autocorrelation indicative of patchiness. Moreover, neither omnidirectional nor directional variograms were able to detect a clear spatial structure in the distribution of either stubble or plowed cornfields in either year. Hence, both habitat types appeared randomly distributed within the landscape at the scale of a 1-km^2 plot. Surface-trend analysis nevertheless revealed that plowed cornfields were slightly more abundant in the northeast section of the study area in 2000.

From 1997 to 2000, we tracked 108 different radio-tagged geese on 292 foraging trips. Distances flown from the roost increased from 1997 to 2000 (means weighed by the number of times an individual was tracked: 22.4 ± 1.7, 22.9 ± 1.3, 27.9 ± 3.2, and 30.4 ± 1.8 km, respectively; YEAR, best model: $w_i = 0.77$; sum of w_i of the models containing this effect = 0.98). Overall, there was no evidence for an effect of roost section on distances traveled from the roost (sum of $w_i = 0.23$). The longest distance recorded for a one-way trip was 62 km. Foraging directions depended on year and roost section ($w_i = 0.47$), while the interaction between these variables did not have a significant effect ($F_{6,280} = 0.3$, $P = 0.95$). Overall, the effect of roost section was strongly supported (sum of $w_i = 0.99$) with directions of birds departing from the roost for foraging trips spreading into a triangle, especially in 1999 and 2000 (Fig. 4).

The fit of the logistic-regression modeling of the probability of choosing a roost section that minimized traveled distances was good ($\chi^2_{132} = 132.0$, $P = 0.45$). This probability depended on year, roost section, and the interaction between the two ($w_i = 0.48$; the second best model retained only the effect of roost section: $w_i = 0.34$; $\Delta AIC_c = 0.34$). The effect of roost section alone was strongly supported (sum of $w_i = 0.90$). The probability that geese selected a section that minimized travel distance was low for the western section in 1997 and 1998 but increased in 1999 and 2000 (Fig. 5). In all years, this probability was low (≤0.45) in the central section, whereas geese departing from the eastern section were minimizing their travel distance most of the time ($P = 0.72$–0.96, varying by year). When geese chose a section that reduced travel distance, the distance saved relative to the worst possible choice varied by year and roost section (the interaction being nonsignificant; $F_{6,280} = 0.6$, $P = 0.76$). A model with an effect of year and the western and eastern sections pooled ($w_i = 0.61$) was supported twice as much as a model with all sections distinct

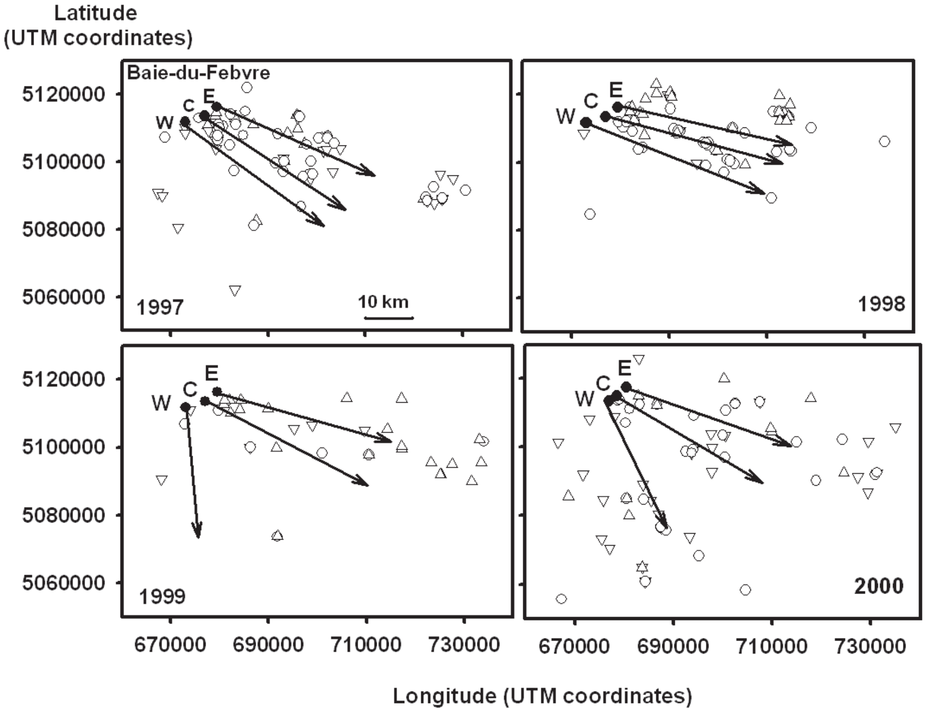

FIGURE 4. Mean trip directions (arrows) and foraging locations (symbols) of radio-tagged Greater Snow Geese flying from the western (W, downward triangles), central (C, empty circles), and eastern (E, upward triangles) sections of the roost in the flooded lowlands of Baie-du-Febvre, 1997–2000. Arrow lengths are independent of the mean travel distances. The center of each roost section is indicated by black circles. UTM coordinates are in meters.

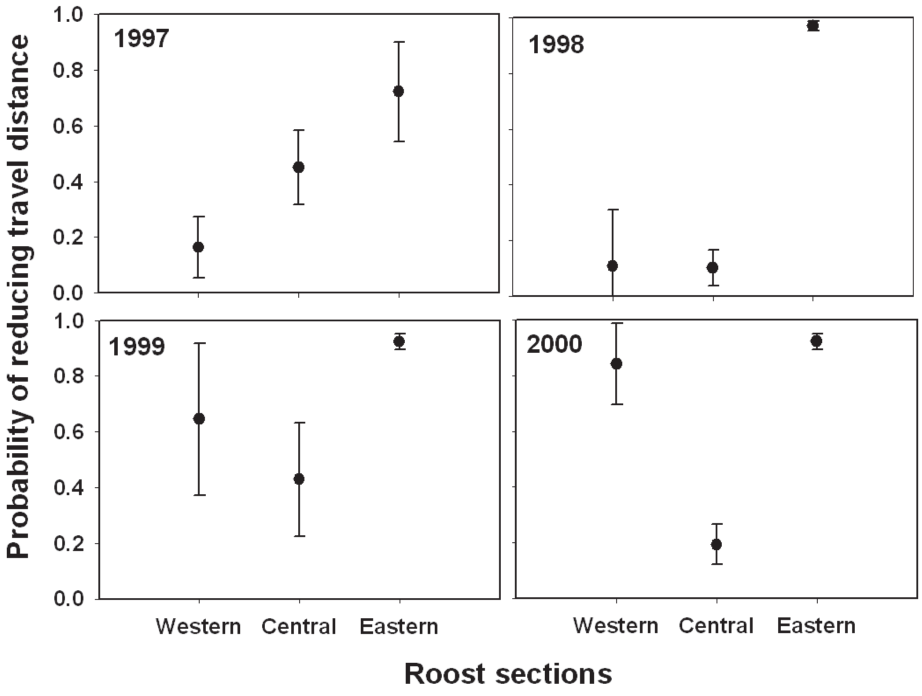

FIGURE 5. Predicted probability (±1 SE) that radio-tagged Greater Snow Geese selected a section of the roost that minimized distance traveled to food patches, 1997–2000.

($w_i = 0.25$; $\Delta\text{AIC}_c = 2.07$) or a model with all sections pooled ($w_i = 0.00$). Over the years, the distance saved by geese that chose the best roost section was 4.5 ± 0.2 km for geese leaving from the peripheral sections and 1.8 ± 0.1 km for geese leaving from the central one. This represented 7–17% of the distance of the average one-way foraging trip recorded during the study (25.9 ± 1.7 km). As observed in 1999 in the western section, however, distance saved could reach up to 26% (7.2 km saved vs. 27.9 ± 3.2 km one way on average).

Overall, between 1998 and 2000, we found no relationship between the probability of minimizing travel distance and fidelity rates observed in the three roost sections ($r_s = -0.24$, $n = 9$, $P = 0.53$). Nevertheless, fidelity rates higher than expected by chance were associated with a reduction in travel distances in the eastern section in 1998 and 2000.

Over the 4 years, 32 geese were tracked for >1 successive days for a total of 22 successive locations with a change of roost section and 33 without. The difference in distance traveled between 2 successive days did not depend on year or on roost-section switch ($w_i = 0.39$; a model adding the effect of roost-section switch was a close competitor: $w_i = 0.28$; $\Delta\text{AIC}_c = 0.68$). Thus switching roost section did not decrease travel distance to foraging sites.

INDIVIDUAL CHARACTERISTICS AND FIDELITY

Relative arrival date and length of stay of geese were not correlated with dominance (date: $r_s = -0.07$, $n = 46$, $P = 0.65$; length: $r_s = 0.06$, $n = 46$, $P = 0.69$), but birds that arrived earlier tended to stay longer ($r_s = -0.22$, $n = 174$, $P = 0.003$). Relative arrival date and length of stay of paired and single geese did not differ (Kruskal–Wallis tests, date: $\chi^2_1 = 0.001$, $n = 104$, $P = 0.97$; length: $\chi^2_1 = 2.574$, $n = 104$, $P = 0.11$). However, single females were of lower dominance rank (20.8 ± 4.8% of won interactions) than paired ones (48.0 ± 6.2%; Kruskal–Wallis test: $\chi^2_1 = 8.0$, $n = 37$, $P = 0.008$).

We identified both the pair status and dominance rank of 37 individuals. Because only four individuals were faithful (33 not faithful) to the western section, we could not analyze factors affecting fidelity to this section. Sixteen geese were faithful (21 not faithful) to the central roost section. Birds that stayed in the area longer were more faithful to this section ($w_i = 0.81$; $\beta = 0.128 \pm 0.055$). Fourteen geese were faithful (23 not faithful) to the eastern section. Our best model retained the effects of year, relative arrival date (RELA), dominance rank (DOM), and the interaction between these two variables ($w_i = 0.70$; the second best model that added the effect of status and length of the staging period was not retained: $w_i = 0.10$; $\Delta\text{AIC}_c = 3.84$). Geese arriving later were more faithful to this section than those arriving early (RELA, $\beta = 0.589 \pm 0.354$). Moreover, dominant birds were less faithful than subordinated birds when arriving late (DOM, $\beta = -0.026 \pm 0.018$) but slightly more faithful when arriving early (RELA × DOM, $\beta = -0.021 \pm 0.011$).

DISCUSSION

Rates of fidelity of Greater Snow Geese to different sections of a roost were higher than expected by chance in 2 years out of 3. The shorter staging period in 1999 coupled with the establishment of a spring conservation hunt in agricultural habitats throughout southern Quebec (Béchet et al. 2004) may have precluded the establishment of roost fidelity that year. Fidelity of individuals to a given winter roost has been shown in several species of geese (Giroux 1991, Wilson et al. 1991). Fidelity to sections within a roost, however, has been documented by only Raveling (1969), who showed that different families of Canada Geese (*Branta canadensis interior*) consistently used distinct portions of a large lake for roosting in winter. Although the staging period is much shorter than winter, Greater Snow Geese had some fidelity to specific roost sections.

Birds departing on foraging trips from different roost sections headed in specific directions, as reported for wintering and resident Canada Geese (Raveling 1969, Schultz et al. 1988). These authors showed a link between roost sections and foraging locations for wintering and resident geese but not for birds staging in fall. In contrast, we detected staging Greater Snow Geese departing from different roost sections using specific directions for foraging trips, and this pattern became established within a few weeks.

Most species of geese travel less than 11 km to reach their feeding sites (see review by Vickery and Gill 1999). Foraging distances that Greater Snow Geese travel on their staging grounds (annual means of 22–30 km with a maximum of 62 km for one-way trips) are among the longest distances recorded. Using allometric equations developed by Rayner (1979) for ducks and assuming that foraging geese are flying at minimum power speed (30.9 km hr^{-1}), we calculated that the minimum flight power is 70.4 W for females with a mean body mass of 2.91 kg in spring (Gauthier et al. 1992). If a staging Greater Snow Goose expends 1350 kJ daily (Thibeault 1994), the distance reduction associated with an appropriate choice of roost section (including the return trip) represents energy savings of 2–5% with a maximum of 9%. As Snow Geese usually complete two foraging trips per day (Béchet et al. 2004), the savings can be doubled. This result supports our initial hypothesis that geese choose a roost section that minimizes travel distance to foraging patches. However, our other prediction that distances traveled in 2 successive days should decrease when a goose switches from one roost section to another was not supported. Hence, minimization of foraging-trip distance may stem simply from the spatial organization of foraging trips from each roost section geometrically reducing the travel distance to food patches on a daily basis.

ROOST CHARACTERISTICS

If intrinsic characteristics enhance fidelity to roost sections, we should expect that larger roost sections located far from roads or woodlots be more attractive for geese because of reduced potential disturbance. In our study this expectation was not met because geese roosting in the eastern and central sections, to which we observed higher fidelity, were closer to the main adjacent road and the woodlots and confined to a smaller area than those roosting in the western section, where fidelity was lower. The situation still persisted in 2000 when we had to shift the three sections eastward. De Koster (1993) found that crop types did not influence within roost use at Baie-du-Febvre, and it is doubtful that the marginal food intake possible at the roost itself influences the use of different sections.

The density of geese in a roost may contribute to its quality through conspecific attraction (Grether and Switzer 2000) and/or reduction in predation risk through a dilution effect (Hamilton 1971), and this may increase fidelity rates. For the European Starling (*Sturnus vulgaris*), Summers et al. (1987) suggested competition for central, more secure positions within a roost. Nocturnal activity of potential predators such as foxes (*Vulpes vulpes*) or coyotes (*Canis latrans*) is difficult to assess, but the low frequency of geese changing roost sections during the night indicates a low level of nocturnal disturbance. Moreover, in several hundred hours of observation, Giroux has rarely noted predators in the Baie-du-Febvre lowlands. Higher fidelity rates observed in the central section in 1998 and 2000 and in the eastern section in 1999 corresponded to sections and years with the greatest use by staging geese. Each year, these two sections covered approximately the same area and were twice as small as the western section. Higher densities and conspecific attraction may have thus favored fidelity to these sections.

SPATIAL ORGANIZATION OF ROOSTING AND FORAGING

The triangular shape generated by the paths of foraging geese departing from the roost, with little overlap, can result from different mechanisms leading to both dispersion and aggregation (Bélisle 1998). Dispersion is predicted by interference models in which foragers distribute themselves among food patches to maximize intake rates while minimizing competition (Fretwell and Lucas 1970, Sutherland 1983). In our study area, this dispersion could be facilitated by cornfields being distributed randomly through the landscape. Dispersion may also result from incomplete information and individual differences in the assessment of the quality of a food patch from the air. On the other hand, aggregation of birds is maintained through flight formation, which can reduce flight costs due to aerodynamic benefits (Speakman and Banks 1998). Aggregation may also result from conspecific attraction, which can help foragers reach a spatial distribution that conforms to the ideal free distribution (Beauchamp et al. 1997). This prediction holds when food patches are not depleted too rapidly and when foragers incur some travel costs, experience low levels of interference, and have to evaluate patch quality, all conditions that prevailed in our study. Geese may also use foraging conspecifics to assess patch quality from the air before joining a flock, a condition observed in the Barnacle Goose (*Branta bernicla*) (Drent and Swierstra 1977). Consequently, the concurrent action of forces causing flock dispersion and aggregation likely explain why geese from the same roost section forage in the same area.

DETERMINANTS OF FIDELITY

Fidelity to a position within a roost may arise because this position is advantageous for finding food. We had predicted high fidelity rates for roost sections that would improve searching efficiency, measured as the probability of reducing distance traveled to food patches. It was only in the eastern section that high fidelity rates were associated with high searching efficiency, so our hypothesis was neither clearly supported nor rejected. Failure to verify this hypothesis may result from the fact that the distance traveled to food patches, though energetically costly, is an incomplete measure of a foraging trip's pay-off. Once geese have started foraging in the fields, energy gains will depend on several factors like resource availability, disturbance rates, and individual differences in foraging efficiency (Bélisle 1998, Caldow et al. 1999).

A longer period of staging in the area may allow the birds to become more faithful to a roost, as shown in the central section. We also found a trend for dominant birds arriving early to be faithful to the eastern section of the roost, but the trend was opposite for subordinate birds. In this section, geese had high probability of minimizing travel distances. Hupp et al. (1996) and Stahl et al. (2001) have shown dominant geese to displace subordinates at high-quality patches. In our case, only dominant birds arriving early maintained fidelity to a roost section that generally reduced travel costs. Through competition for space, dominant birds may have prevented late-arriving birds (dominant or not) from having fidelity to this section.

We conclude that a goose's position within a roost is in part determined by conspecific attraction, in some cases by a significant reduction in costs of travel to food patches, and by the effect of individual differences in dominance rank. Fidelity of Snow Geese to sections of a roost may thus result from the concurrent and combined effects of these three factors.

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